

EXPERIMENTAL TAXONOMY IN THE GENUS  
*AMELANCHIER*. II:  
DO THE TAXA IN THE GENUS *AMELANCHIER*  
FORM AN AGAMIC COMPLEX?

W. ANN ROBINSON

According to Wiegand (1912) our major herbaria contained almost as many transitional sheets as sheets typical of the supposed species in the genus *Amelanchier*. In fact, many taxonomists have been inclined to believe that no specific lines exist in this genus. McVaugh (1946) stated:

“the multiplicity of forms in *Amelanchier* (as also in *Crataegus*, *Malus*, *Rubus* and other genera) is so great as to defy taxonomy based on herbarium material alone. I think we shall not arrive at any satisfactory scheme of classification of these genera until we know more about their genetical peculiarities.”

With this goal in mind the following hypothesis is suggested. The taxa in the genus *Amelanchier* form an agamic complex not unlike that existing within several genera of the Maloideae: *Crataegus*, *Malus*, and *Sorbus*. Babcock and Stebbins (1938) suggested that the only basis for a satisfactory treatment of agamic complexes was an understanding of the role that the three processes, polyploidy, hybridization, and apomixis have played in their formation.

Polyploidy is considered to have played a prominent role in the evolution of this genus as diploid, triploid, and tetraploid forms commonly appear in the *Amelanchier* of the northeastern United States (Robinson & Partanen, 1980).

Experimental studies into the breeding methods of *Amelanchier*, however, have been relatively meager. Both Wiegand (1912) and Nielsen (1939) described from field observations the apparent ease with which the species of *Amelanchier* hybridize; neither, however, performed confirmatory experiments. Cruise (1964) measured the extent of hybridization in three eastern *Amelanchier* species with the utilization of Anderson's hybrid index. Harris (1970) reported that interspecific crosses have been performed at the Beaverlodge Experimental Station with *Amelanchier alnifolia* Nutt., the common species of the western United States, but the experimental data



were not included in this paper. Harris (1970) also suggested that most plants of *A. alnifolia* are self-fertile.

Kirshner (1890) may have been the first to suggest self-fertility in *Amelanchier* when he wrote: "In den schräg stehenden Blüten kann spontane Selbstbestäubung leicht durch herabfallenden Pollen erfolgen." McKay (1973) indicated that self-compatibility existed in several of the eastern *Amelanchier* species from observations of plants naturally occurring in Ontario, Canada. Her experiments, however, are not completely comparable to the present study, for emasculation involved only removal of the anthers, and the types of self-compatibility, autogamy and geitonogamy, were not differentiated.

The question of apomixis in *Amelanchier* has had few published references. McVaugh (1946) suggested parthenogenesis as a possible explanation for the confusion in this genus. McKay (1973) emasculated 43 flowering *Amelanchier* racemes and found 12 percent of the racemes showed successful seed set. Her experiments, however, did not differentiate parthenocarpy with aborted seeds from apomictic seed formation. In 1974 Robertson made the statement that, unlike *Crataegus*, apomictic clones are not known in *Amelanchier*. Since *Sorbus* and *Malus* were reported by Stebbins (1941) to have SA + P (somatic apospory + parthenogenesis) type of apomixis, the experiments in this paper were formulated to test for its existence in the genus *Amelanchier*.

#### PROCEDURE

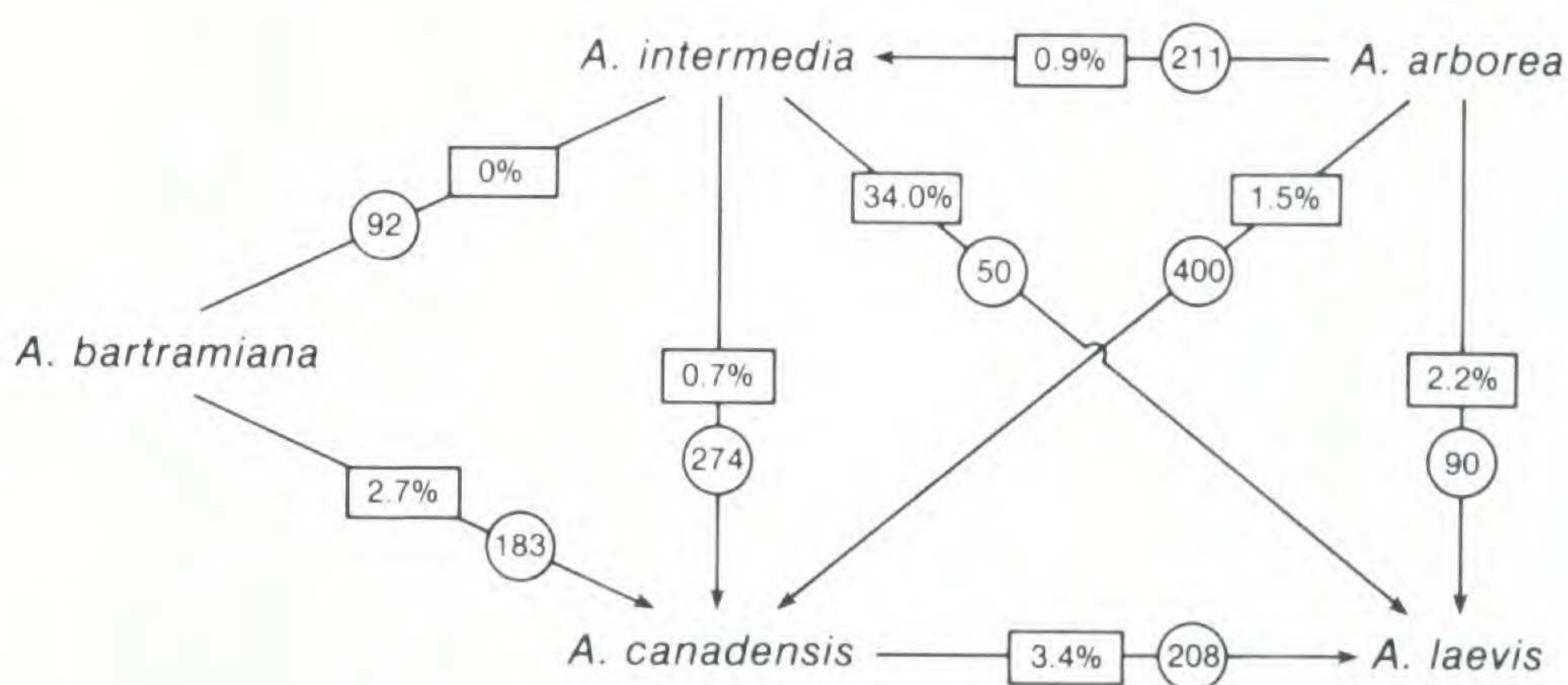
Considering that the number of species comprising *Amelanchier* is unsettled, it seems wisest to follow the taxonomy of Fernald (1950), who recognized the most species in the northeastern United States. This should afford the greatest amount of expected genetic variation. The validity of these species will be explored in future studies. The experiments in this study have therefore been confined to the following species:

- A. amabilis* Wieg.
- A. arborea* (Michx.f.) Fern.
- A. bartramiana* (Tausch) Roemer
- A. canadensis* (L.) Medic.
- A. gaspensis* (Wieg.) Fern. and Weath.
- A. humilis* Wieg.



*A. intermedia* Spach  
*A. laevis* Wieg.  
*A. nantucketensis* Bickn.  
*A. obovalis* (Michx.) Ashe  
*A. sanguinea* (Pursh) DC.  
*A. stolonifera* Wieg.  
*A. wiegandii* Nielsen

Figure 1  
 Hybridization trials with the species of the *Canadensis* complex



- A line between two species indicates that cross-pollination has resulted in fruit set. (If not reciprocal, arrow points to pistillate parent).
- Absence of a line between two species indicates that cross-pollination has resulted in no fruit set.
- The number in the rectangular box denotes the percentage of flowers resulting in successful fruit set, with normal seed formation.
- A question mark preceding the percent indicates fruit was set, but it was damaged by predators.
- The number enclosed in the circle indicates the number of flowers that were cross-pollinated.

The original goal was to collect one living plant of each species and more if possible. These were moved, beginning in 1970, to Monroeville, Pa. where ecophenic variation would be minimized in a uniform environment. By separation of a portion of the stoloniferous clump or by division of the fastigate forms one can readily transplant specimens of *Amelanchier*, with the new and former specimens continuing good growth. The original collection sites of the plants utilized in this study are enumerated in the appendix. Voucher specimens of all material utilized have been deposited in the Carnegie Museum Herbarium (CM).



There has been a 67.9% survival rate following transplantation, with a total of 40 plants presently under observation. Unfortunately, two plants of *Amelanchier gaspensis* died before experiments could be performed and this species could not be included in the present study. A single plant of *A. amabilis* was successfully transplanted but has yet to flower. Transplantation frequently appears to delay flowering by three to four years.

If hybridization is as common as suspected in *Amelanchier*, there exists the possibility that plants of hybrid origin, or plants having undergone introgression, could have been introduced into cultivation. Close morphological observations and pollen stainability with cotton blue in lactophenol were utilized as indicators of possible hybridization. All specimens suspected as being of hybrid origin were eliminated from the breeding experiments, except for plants of *A. wiegandii* and *A. sanguinea*, with 39.3% and 37.6% pollen stainability respectively. These plants were retained in the study with the thought of evaluating their relationships to the other species and with the prospect of a review of their evolution and taxonomic status.

As the routine morphological observations were made, the plants appeared to fall into two morphological complexes (Robinson & Partanen, 1980). *Amelanchier bartramiana*, with its distinctive single or few flowered raceme, does not fit comfortably in either complex but is included in the Canadensis complex because of its diploid nature.<sup>1</sup> The morphological traits appear to be correlated with a change in ploidy level, the Canadensis complex representing diploid taxa and the Sanguinea complex triploid and tetraploid taxa. The only taxa observed to be exceptions to this hypothesis are *A. intermedia* and *A. obovalis* in which both diploid and triploid plants are found.

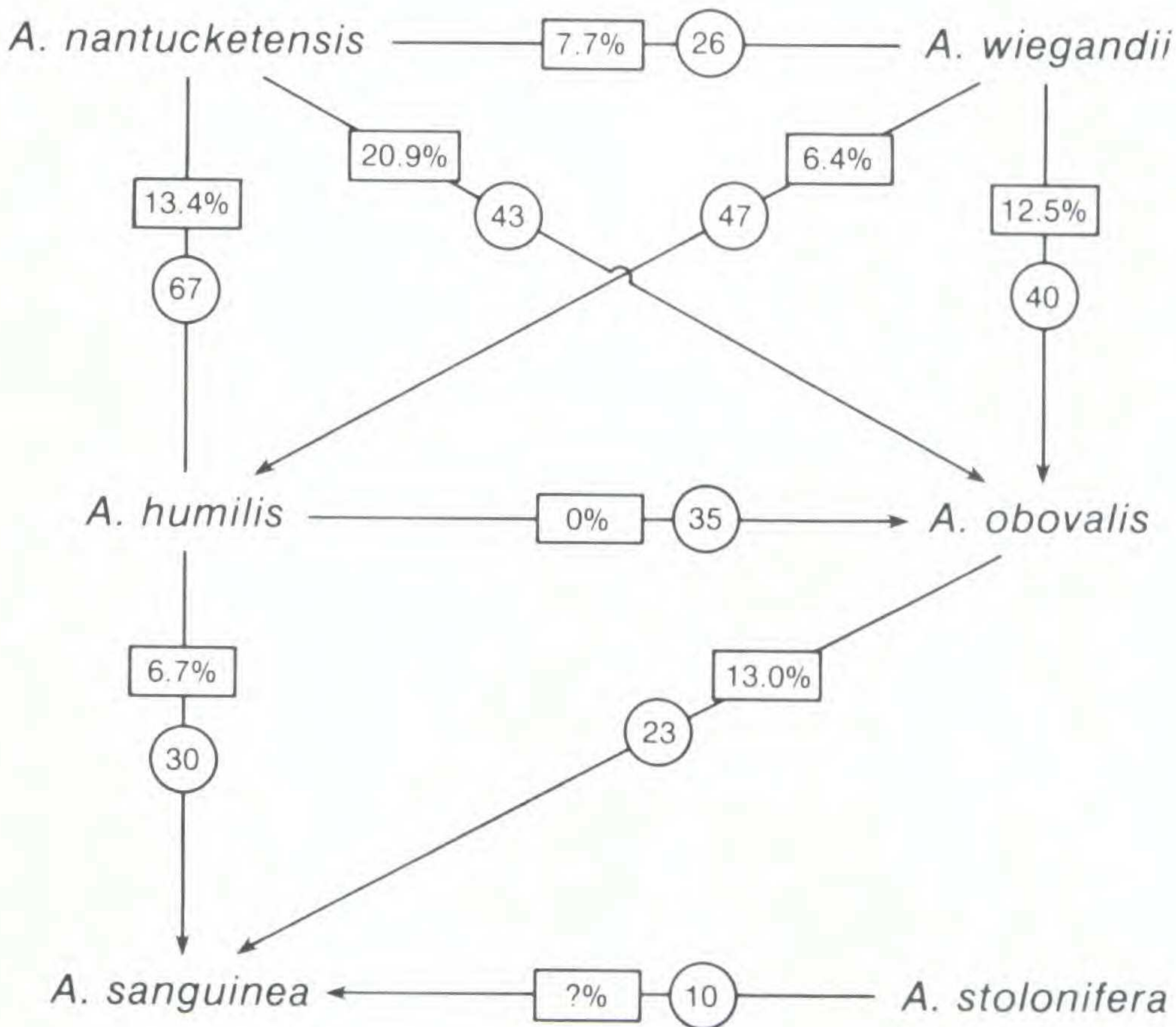
The following procedure was utilized in all the experiments to investigate the possible existence of apomixis, self-compatibility, and hybridization in the *Amelanchier* taxa growing in the northeastern United States. When autogamy was investigated, it was without emasculation and without the application of pollen. Single flowers were covered by bags constructed of seamless cellulose dialysis tubing, at least 48 hours prior to anthesis. The dialysis bag, in this case and in all the experiments to be enumerated, remained in

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<sup>1</sup>Löve and Löve (1966) have reported tetraploid individuals.



Figure 2  
Hybridization trials with the species of the Sanguinea complex<sup>3</sup>



<sup>3</sup>*A. stolonifera* × *A. obovalis* and *A. stolonifera* × *A. wiegandii* have not been attempted.

place until pollination was complete. This is extremely important for although *Amelanchier* has been considered entomophilous and allophilic (Cruise, 1964), experiments by Landridge (1969) have indicated significant airborne pollen in the closely related genus *Malus*. Upon removal of the dialysis bag, a bag constructed of fiberglass screening was substituted. This is necessary for the collection of dehisced immature fruit and for protection against predators seeking partially ripe fruit. *Amelanchier* has been noted to experience the "June Drop" phenomenon found in other Maloideae (Heinicke, 1917).



To test for apomixis, geitonogamy, xenogamy, and interspecific hybridization, emasculation was performed 48 hours prior to anthesis. Although the northeastern United States taxa of *Amelanchier* are largely protogynous<sup>2</sup>, occasionally the anthers dehisce prior to anthesis. Kenneth Robertson and Robert Simonet (both pers. comm.) also mentioned this possibility. When any evidence of early anther dehiscence was noted at the time of emasculation, the flowers were not utilized in the experiments. Emasculation involved removal of the superior floral cup (sepals, petals, and stamens) under magnification with a cutting edged needle. Such emasculation is much more feasible, rapid, and reliable than simply removing the anthers. Nyéki (1974) found no significant difference between fruit set in pear flowers subjected to radical emasculation, and those deprived only of their anthers. Immediately following emasculation the pollen appropriate to the experiment was applied utilizing the entire stamen removed from the isolation of a dialysis bag. The filament was held by tweezers and the dehisced anther brushed against the stigmas. The racemes were then enclosed in a dialysis bag. The pollen applied following emasculation remains on the stigma and is ready to germinate as soon as conditions are favorable. It was impossible because of the varying number of flowers available on the plants and the varying flowering times to have identical numbers of flowers of each plant species for the individual experiments. The data are summarizations of experiments performed different years, various days, and numerous times of the day.

Seed germination was tested initially in the laboratory. Fungal growth proved to be a marked problem even after cleaning by agitation, surface disinfectants, and fungicides. Since the factors involved in breaking dormancy can be quite complex and since germination in these early experiments never exceeded 8.1%, the decision was made to follow the normal stratification pattern presently successfully undergone by seeds under the influence of the vagaries of the weather in the north temperate zone.

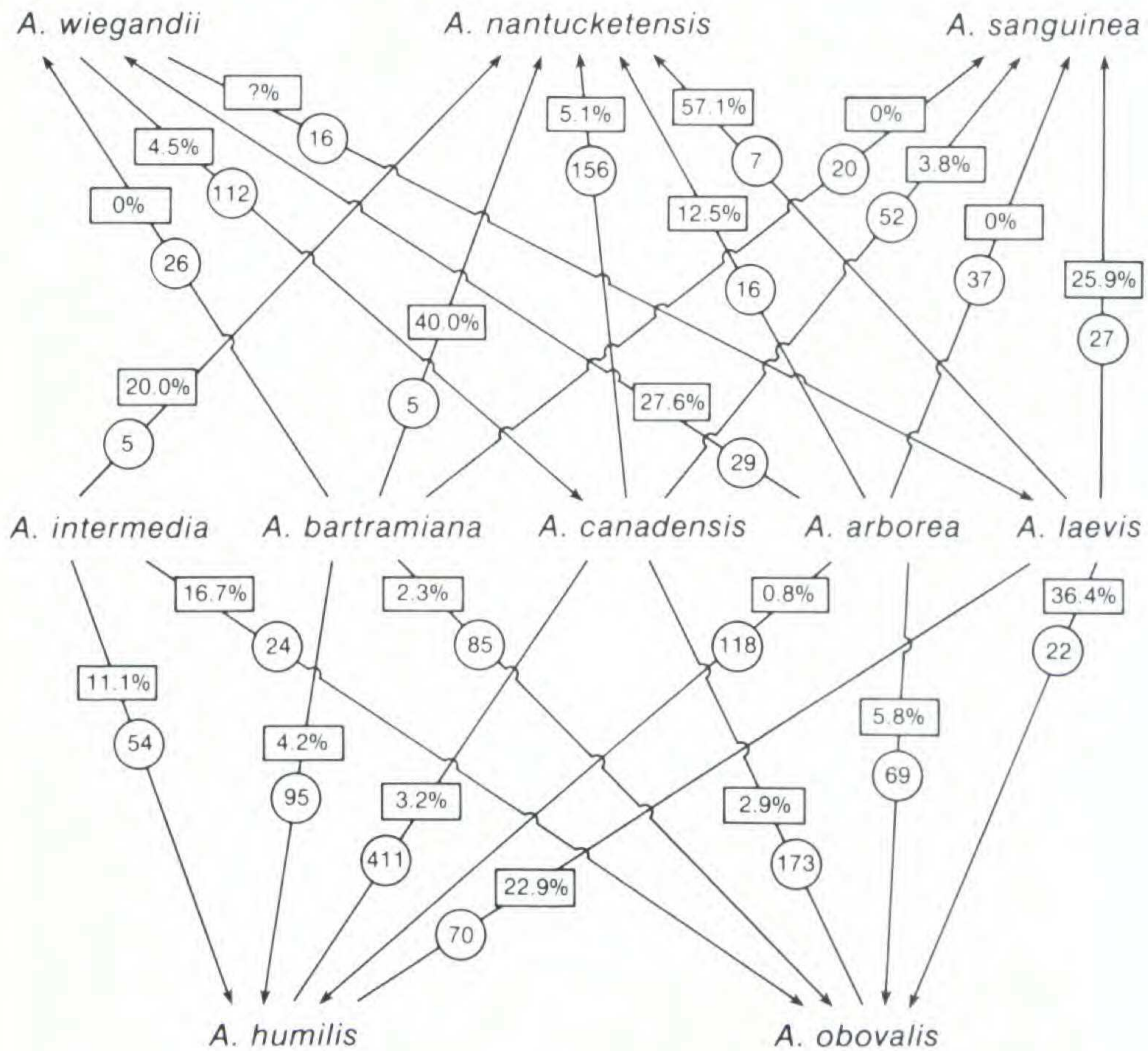
All seeds were planted in sifted soil in peat pots and placed directly in the ground soon after they would have normally fallen to the ground. Seedlings do not appear until the following spring.

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<sup>2</sup>In Europe *A. canadensis* (*A. botryapium* DC.) was noted to be slightly protogynous by Kirshner (1890).



Figure 3  
Hybridization trials between the species of the Sanguinea complex  
and the species of the Canadensis complex



A list of parental samples and results of individual crosses is available on request from the author.

#### RESULTS

Prior to 1977, only one species, *A. humilis*, formed fruit with apparently mature seed following emasculation to test for apomixis. Of the 1731 flowers of *A. humilis* emasculated only 0.58% formed fruit with mature seed, and this seed failed to germinate. Since this exceedingly low figure could have been in the range of experimental error, during the 1978 and 1979 seasons, these experiments were markedly extended. In 1979 one added technique was initiated. Following emasculation and prior to covering with the dialysis bag, the stigmas were dusted with the pollen of *Tussilago farfara* L. This



species-alien pollen was selected due to its abundant availability at the time of flowering. This technique was adopted since Frankel and Galun (1977) had reported that the stimulation of pollination is required for apomictic seed development in apple. In 1978 and 1979 a total of 2100 flowers were emasculated with no resulting fruit formation with mature seed. It therefore seems reasonable to assume that the SA + P type of apomixis does not occur in the northeastern forms of *Amelanchier*.

The results of the experiments to check for the two types of self-compatibility are shown in Table 1. First, it is important to state that all the plants in this study have had fruit production with normal seed following open-pollination. Therefore, we are investigating plants with a potential for seed formation under the appropriate conditions. Plants of *Amelanchier arborea* and *A. stolonifera* produced no fruit with normal seed following autogamous and geitonogamous pollination. The attempted pollinations of *A. stolonifera* are too few to make any positive statement. However, in the case of *A. arborea* it can be stated with a degree of subjectivity that the specimens investigated in this study are self-incompatible. Although it is difficult to discern with absolute accuracy (see Table 1), it appears that the Sanguinea complex has a higher potential for self-compatibility than the Canadensis complex. This is even more apparent from the seed germination attempts (Table 2). The seeds resulting from autogamous and geitonogamous pollinations within the Canadensis complex failed to germinate. Within the Sanguinea complex, seedlings of *A. obovalis* and *A. humilis* from autogamous pollinations and *A. nantucketensis* from a geitonogamous pollination are presently growing. A seedling of *A. wiegandii* from a geitonogamous pollination died the summer following its germination.

Comparing the results of the xenogamous pollinations with those of autogamy and geitonogamy, the overall impression emerges that xenogamous pollinations result in a higher percentage of normal seed. It should be noted (Table 1) that *A. arborea* still did not form normal seed, but following xenogamous pollination fruit did form but with immature and aborted seeds. The seedlings from the xenogamous crosses are double the number from self-compatibility crosses and crosses between species and are generally healthy and vigorous. There are five seedlings from *A. humilis* × *A. humilis* and six seedlings from *A. canadensis* × *A. canadensis* crosses.



Table 1  
Optional breeding methods

Species	Types of pollination					
	Autogamous		Geitonogamous		Xenogamous	
	No. flowers pollinated	No. resulting fruit with mature seed	No. flowers pollinated	No. resulting fruit with mature seed	No. flowers pollinated	No. resulting fruit with mature seed
Canadensis complex						
<i>A. arborea</i>	84	*	81	*	98	0**
<i>A. canadensis</i>	234	3	296	3	364	35
<i>A. intermedia</i>	54	4	57	9	36	2
<i>A. laevis</i>	36	1	98	10	15	***
<i>A. bartramiana</i>	12	2	22	3		
Sanguinea complex						
<i>A. humilis</i>	111	26	46	6	173	22
<i>A. nantucketensis</i>	15	0**	12	4	12	5
<i>A. obovalis</i>	46	6	14	5	73	13
<i>A. sanguinea</i>	4	1	44	***		
<i>A. stolonifera</i>	1	*	6	*		
<i>A. wiegandii</i>	5	1	16	6		

- \* All flowers dried up  
 \*\* Fruit with immature and aborted seeds  
 \*\*\* Fruit set, but destroyed by predation



Table 2. Results of germination trials with seeds from autogamous, geitonogamous, and xenogamous pollinations

	autogamous		geitonogamous		xenogamous	
	Total No. Seeds	No. Seeds Germinated	Total No. Seeds	No. Seeds Germinated	Total No. Seeds	No. Seeds Germinated
Canadensis complex						
<i>A. canadensis</i>	3	0	12	0	84	7
<i>A. intermedia</i>	5	0				
<i>A. laevis</i>	2	0				
Sanguinea complex						
<i>A. obovalis</i>	9	1	10	0	21	4
<i>A. humilis</i>	40	2	12	0	36	5
<i>A. nantucketensis</i>			23	5	4	0
<i>A. wiegandii</i>	2	0	5	1		
<i>A. sanguinea</i>	1	0				



The results of the interspecific crosses are detailed in figures 1–3. Every combination has been attempted except for two: *Amelanchier stolonifera* × *A. obovalis* and *A. stolonifera* × *A. wiegandii*. The lack of a line between the two species, therefore, indicates fruit did not set following hybridization with the above two exceptions. Considered as a whole, a total of 336 apparently mature normal seed resulted from 3622 interspecific crosses. With the exception of the seeds from the interspecific crosses listed in Table 3, seed germination has failed. One can also note from Table 3 that 54.5% of the seedlings died during the first year. The three hybrid seedlings, *A. canadensis* × *A. arborea*, that grew from seeds planted during the late summer of 1972 have exhibited remarkably rapid growth and vigor. They flowered for the first time in 1977 but have yet to set fruit following open pollination or in experiments to test for apomixis or autogamy. The pollen stainability of the three plants has been 91.9%, 92.6%, and 94.8% respectively, with observations made the same day and hour for each plant.

#### DISCUSSION

With the possibility that *Amelanchier* taxa form an agamic complex, the three processes considered to operate in such a complex (Stebbins, 1950) will be discussed in turn: apomixis, hybridization, and polyploidy.

On the basis of the experiments in the present study, it can be stated with a reasonable degree of assurance that the SA + P type of apomixis does not occur in the northeastern forms of *Amelanchier*.

Table 3. Germinated seeds from interspecific hybridization

Interspecific cross	Total No. Seeds	No. Seeds Germinated	Seedling Survival To 1 Yr.
<i>A. canadensis</i> × <i>A. intermedia</i>	4	1	0
<i>A. canadensis</i> × <i>A. arborea</i>	22	3	3
<i>A. obovalis</i> × <i>A. nantucketensis</i>	13	3	0
<i>A. obovalis</i> × <i>A. canadensis</i>	3	1	1
<i>A. obovalis</i> × <i>A. intermedia</i>	6	1	0
<i>A. humilis</i> × <i>A. laevis</i>	16	1	0
<i>A. wiegandii</i> × <i>A. arborea</i>	16	1	1



Muniyamma and Phipps (1979) state that apparently sexual endosperm is necessary in *Crataegus* for apomictic seed development and that *Crataegus pruinosa* (Wendl.) K. Koch, *sens. lat.* has Sa + Ps (somatic apospory + pseudogamy) type of apomixis. Further experiments are being initiated to evaluate its occurrence in *Amelanchier*.

Is it necessary, however, to consider that agamospermy must exist for the presence of an agamic complex in a genus? Following the classification of Gustafsson (1946), vegetative reproduction could be considered an apomictic phenomenon. Perpetuation of unbalanced chromosome forms by self-compatibility and vegetative reproduction, and the similar longevity of hybrid microspecies with occasional fertile gametes and vegetative reproduction, could give the typical morphological appearance of an agamic complex. The discontinuities of the diploid species would be obscured by the hybrid derivatives and polyploids. With the exception of *Amelanchier sanguinea* and *A. wiegandii* the members of the Sanguinea complex have been observed to form stoloniferous clumps. The remaining taxa included in this study can reproduce by shoots from their root systems. Frequently a single dead tree trunk will be replaced by a multi-trunked shrub. Excluding the possibility of major environmental change all of the taxa in the northeastern United States could maintain themselves by asexual vegetative reproduction.

Following study of the *Amelanchier* specimens from the major eastern herbaria the Wiegand estimation (1912) that a third of the sheets were hybrids soon seems most valid. From field observation, however, a 33% rate of hybridization seems inordinately high. With a search for the unusual and different specimens in *Amelanchier*, plant taxonomists have collected a disproportionate number of hybrids. Hybrids occur with the greatest frequency in the pioneer shrub community in the succession following burning, deforestation, or the abandonment of farm land. Although these areas are more frequent following the activities of man, they are less common than the preferred environment in the forest community of the Mixed Mesophytic Forest Region and the Hemlock-White Pines-Northern Hardwoods (Braun, 1950). Occasionally *Amelanchier* will grow in the relatively shaded understory of the mature forest, but it seems to prefer sun light and less competitive edge communities, such as the abundant hillsides and stream banks found throughout



the northeastern United States. In addition, the results of the present study indicate that although interspecific pollination, fertilization, and seed formation have the potential to occur, hybrid establishment may be a far less common occurrence (Fig. 3 & Table 3). Although the percentage of hybridization is realistically less than 33%, it is a viable evolutionary pattern, and numerous hybrid swarms of *Amelanchier* taxa are found in disturbed and intermediate habitats.

A statement by Levin (1971) should be mentioned. He notes that the failure to take cognizance of the competitive status of pollen from different sources could lead to erroneous conclusions about the facility with which species hybridize or exchange genes in nature. He states that domestic pollen advantage ostensibly is the rule rather than the exception. Knight (1917) and Cooper (1938), however, reached the opposite conclusion from work with apple. They found that pollen tubes from autogamous pollinations grew more slowly than those from intra-varietal crosses. Further research is required before this point can be evaluated in the genus *Amelanchier*.

Studying the species of the northeastern United States, Robinson and Partanen (1980) indicated that *Amelanchier* contains diploid, triploid, and tetraploid taxa. Although the authors noted the frequent appearance of multivalents and univalents at metaphase I, the plants studied set fruit in open-pollination and the pollen stained generally in excess of 85% with cotton blue in lactophenol. Since *Amelanchier* along with the other Maloideae is considered to be a secondary polyploid (Stebbins, 1950), it apparently readily tolerates the loss of an occasional chromosome.

In the present study, however, several factors indicate a reduced gametic fertility of the polyploid taxa probably attributable to abnormal chromosome segregation. In figure 3 one notes that the role of the pistillate parent is achieved almost exclusively by the polyploid taxa of the Sanguinea complex in crosses with the diploid taxa. This probably reflects a reduced viability of the microgametes of the polyploid taxa, a phenomenon noted by Darlington (1937). In addition, the apparent higher potential for self-compatibility (Table 1) and vegetative reproduction in the polyploid Sanguinea complex could have resulted from the selective advantage of these types of reproduction to plants with reduced viability of microgametes.

Although caution is necessary when studying only a portion of



the taxa in a genus of world-wide North Temperate distribution, the overall impression is emerging that the species of the genus *Amelanchier* represent an agamic complex with polyploidy, hybridization, and asexual vegetative reproduction being major forces in its evolution. The present studies will be extended beyond a regional basis and it is hoped that a clearer picture of the problem will emerge. In this regard, the author would be pleased to receive semi-dried fruit of all *Amelanchier* taxa from documented sources world-wide for propagation and experimentation.

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W. ANN ROBINSON  
4264 NORTHERN PIKE  
MONROEVILLE, PA 15146

#### APPENDIX

List of and collection data for the taxa utilized in this study. (R) = the author's collection.

- A. amabilis* Wieg. N.Y., Ontario Co., 2.5 mi. S. of Vine Valley,  
*R* 163
- A. arborea* (Michx.f.) Fern. W. Va., Jefferson Co., Key's Gap,  
*R* 93; Pa., Fayette Co., 4.1 mi. S. of Elliottsville, *R* 108



- A. bartramiana* (Tausch) Roemer Pa., Monroe Co., shore of Lake Naomi, Naomi Pines, *R 120*; Pa., McKean Co., 5 mi. W. of Kane, *R 168*
- A. canadensis* (L.) Medic. N.J., Ocean Co., off Rt. 539, 3.6 mi. S. of Rt. 72, *R 111*; N.J., Ocean Co., off Rt. 539, 0.1 mi S. of Rt. 530, *R 113*; N.J., Burlington Co., off Rt. 537, 2.8 mi. W. of Ocean Co. Line, *R 114*; N.J., Ocean Co., off Rt. 537, 0.3 mi. W. of intersection of Rts. 537 and 526, *R 115a*; N.J., Middlesex Co., within cloverleaf of intersection of Rts. 18 and 9, *R 116*; Maine, York Co., Berwick, *O.M. Neal, Jr. 131*; Mass., Norfolk Co., crest of Blue Hill, Milton, *R 157*; Va., Henrico Co., at intersection of Rt. 164, Highland Springs, *R 159*.
- A. gaspensis* (Wieg.) Fern. and Weath. Maine, Aroostook Co., off Rt. 210, ¼ mi. E. of Rt. 1, Presque Isle, *Margaret Hurst 145*.
- A. humilis* Wieg. W. Va., Monongalia Co., Old Kingwood Pike, *Dr. and Mrs. H. A. Davis 132*; Maine, Penobscot Co., N. W. side of Rt. 43, 2 mi. off Rt. 195 at Old Town Exchange, *R 148*.
- A. intermedia* Spach Pa., Pike Co., off Rt. 6, 5.7 mi. E. of junction of Rt. 6 and Rt. 739, *R 119*.
- A. laevis* Wieg. Pa., Susquehanna Co., Old McConnell farm, near Lakeside, *R 124*; Pa., Bedford Co., Wolf Swamp, Hyndman Quadrangle, 39°52'30" and 78°44'30", *R 160*; W. Va., Randolph Co., Red Run, W. of Cheat Bridge, *R 161b*.
- A. nantucketensis* (Bickn.) Mass., Nantucket Co., Nantucket Isl., Nantucket R. R. bed, near Inquirer-Mirror office building, *R 155*; Conn., New London Co., N. E. side bridge Alewife Cove, Waterford, *R 156*.
- A. obovalis* (Michx.) Ashe Pa., Lackawanna Co., cliff overlooking DLWRR, ½ mi. E. of Old Forge, *R 122a*; 500' E. of *R 122a*, *R 122b*; Pa., Luzerne Co., off Rt. 307, crest Penobscot Knob, *R 123a*.
- A. sanguinea* (Pursh) DC. W. Va., Pendleton Co., North slope North Fork Mt., *R 128 b*.
- A. stolonifera* Wieg. Maine, Waldo Co., Fort Point, Cape Jellison, Stockton Springs, *R 149*.
- A. wiegandii* Nielsen Maine, Waldo Co., Fort Point, Cape Jellison, Stockton Springs, *R 150b*.